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A CONTRIBUTION TO THE BIOLOGY OF THE
GIGANTURIDAE, WITH DESCRIPTION OF A NEW
GENUS AND SPECIES

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No.10— *A Contribution to the Biology of the Giganturidae,
with Description of a New Genus and Species*¹

BY VLADIMIR WALTERS

INTRODUCTION

The morphology of the giganturid fishes is imperfectly known. Brauer (1908) described the structure of the eye of *Gigantura indica*, and Bierbaum (1914) worked out the structure of the labyrinth of *G. chuni*. The osteology of *G. vorax* was studied by Regan (1925). While preparing an account of the Giganturidae for a forthcoming volume of "Fishes of the Western North Atlantic" I found it necessary to investigate the anatomy of the specimens, since many of their external features had been destroyed.

William C. Schroeder and Mrs. Myvanwy Dick of the Museum of Comparative Zoology, and James E. Morrow of the Bingham Oceanographic Laboratory generously loaned their specimens of *Gigantura vorax*. Through the kindness of Carl L. Hubbs and Alfred Ebeling of the Scripps Institution of Oceanography, two specimens of unidentified Pacific giganturids were borrowed for comparison with *G. vorax*. I am grateful to N. B. Marshall of the British Museum (Natural History) who examined the types of *G. vorax* Regan and *G. gracilis* Regan both in the British Museum and in the Dana collections in Copenhagen. An expression of appreciation is due Giles W. Mead of the Museum of Comparative Zoology who provided his manuscript revisions of five families of iniomous fishes, and who forwarded material belonging to various synodontoid genera. James E. Böhlke of the Academy of Natural Sciences at Philadelphia, Daniel M. Cohen of the U. S. Fish and Wildlife Service, Giles W. Mead, and William A. Gosline of the University of Hawaii critically read this manuscript. The sections dealing with the nervous system, sense organs and sensory cues were read by Lester R. Aronson of this Museum, and his suggestions and criticisms are appreciated. Samuel B. McDowell, Jr. aided in some of the dissections and interpretations of structure,

¹A more general account of the Giganturoidea will appear in Part 4, "Fishes of the Western North Atlantic." Parts of these giganturid studies have been supported by funds granted by the National Science Foundation (N.S.F. Grant 7123) to the Sears Foundation for Marine Research, Yale University.

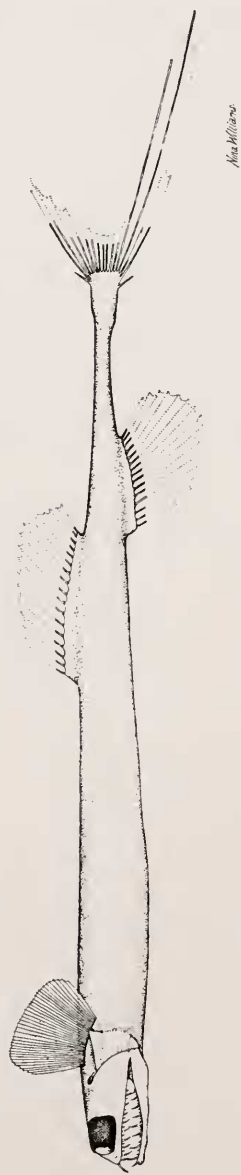


Figure 1. *Bathyleptus lisae*, reconstructed from holotype.

including examinations of members of other groups which formed the background for the phylogenetic assessment of the Giganturidae. The drawings were made by Nina Williams and Samuel B. McDowell, Jr.

Some of my observations (on other species) are at variance with Regan's (1925) diagnosis of *Gigantura* and with his osteological account of *G. vorax*. For instance, none of my specimens have vomerine teeth while *G. vorax* is said to have two vomerine teeth, one behind the other; in *G. vorax* the scapula bears some

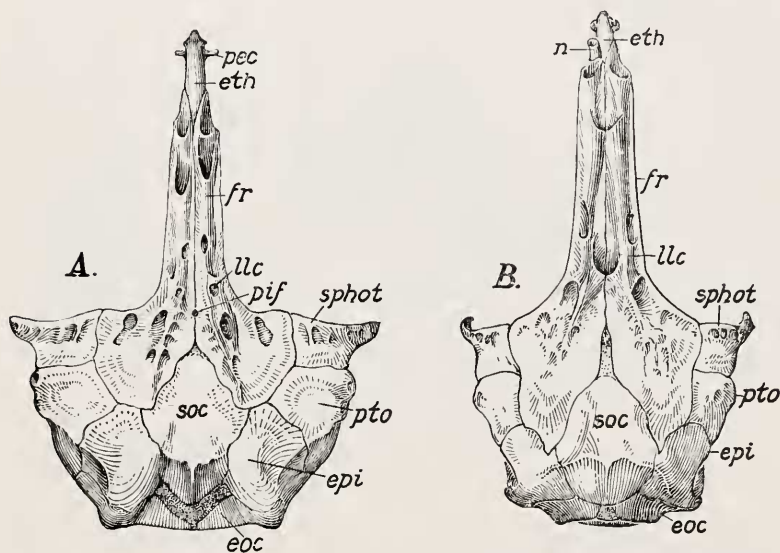


Figure 2. Skull in dorsal aspect. A. *Bathyleptus lisae*, holotype. B. *Gigantura vorax*, American Museum of Natural History 20393. See legend of Figure 3 for key to abbreviations.

of the fin-rays, the cleithrum extends the full length of the girdle and there is no posterior coracoid process, while in my material the scapula does not support any fin-rays, there is no cleithrum, and the coracoid bears a posterior process. Marshall's re-examination of Regan's material (both *gracilis* and *vorax*) failed to disclose vomerine teeth, and the pectoral girdle, which Regan illustrated, has either been discarded or lost. Marshall also believes that the neurocranium of the type of *G. vorax* more closely resembles the figures given below than it resembles Regan's figures.

MORPHOLOGY

(Figures 2 to 7)

Visceral Arches. All that remains of the hyoid arch in *Gigantura* and *Bathyleptus* are the hyomandibular and the quadrate; the ventral elements of this arch and the branchiostegal rays are absent. There do not seem to be any cartilages either supporting or associated with the gills. In both genera the first gill slit is the longest and lenticular, the second is shorter and elliptical,

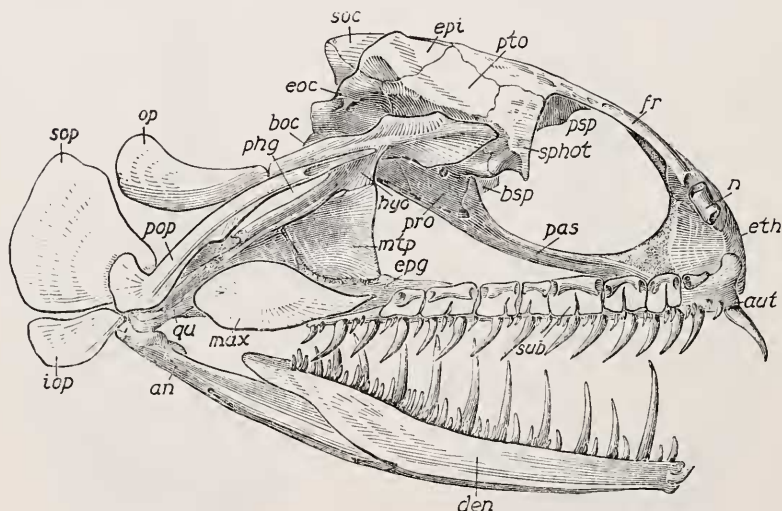


Figure 3. Skull of *Gigantura vorax* in lateral aspect, composite. Abbreviations: an, angular; aut, autopalatine; boc, basioccipital; bsp, basisphenoid; den, dentary; eoc, exoccipital; epg, ectopterygoid; epi, epiotic; eth, mesethmoid; fr, frontal; hyc, hyomandibular; iop, interopercular; llc, supraorbital lateralis canal; max, maxilla; mtp, metapterygoid; n, nasal; op, opercular; pas, parasphenoid; pcc, preethmoid cornu; phg, preopercular-hyomandibular gap; pif, pineal foramen; pop, preopercular; pro, prootic; psp, pterosphenoid (alisphenoid); pto, pterotic; qu, quadrate; soc, supraoccipital; sop, subopercular; sphot, sphenotic; sub, suborbital (?).

the third is shorter and D-shaped, the fourth is very small and circular, and there is no slit behind the hemibranch. In both genera the anterior set of pharyngeal teeth is in the roof of the pharynx behind the last gill slit and anterior to the suspensoria, while the posterior set is in the roof of the esophagus

medial to the kidneys. The posterior pharyngeal arch is the most complete of the post-mandibular arches, consisting of a backwardly directed pharyngobranchial cartilage (toothed), epibranchial and ceratobranchial cartilages in line and sloping downward and backward, and a forwardly-directed hypobranchial cartilage. There is no basibranchial cartilage. The appearance of this arch is Z-shaped. The anterior set of pharyngeal teeth connects with the posterior set, and presumably represents the pharyngobranchial part of the last gill arch.¹

Viscera. In both genera the kidneys are in the body wall between the epaxial and hypaxial musculature close behind the pectoral girdle; they are triangular and pale-colored with discrete black spots. The anterior location of the kidneys indicates that they may be pronephric, though they are not near the heart. The excretory ducts follow retroperitoneal paths lateral to the mesogasters and enter the urinary bladder beneath the dorsal fin; the bladder discharges to the outside through a urinogenital papilla. The ovaries are hollow sacs, fused posteriorly, and in *Gigantura* they either discharge into the urinary duct below the bladder or open to the outside so close to the bladder that separate openings (if these exist) could not be found in the material examined. The gross anatomy of the male urinogenital system is unknown. In *Bathyleptus* the gonads are missing from both specimens and the excretory duct cannot be traced much beyond the rear of the stomach.

In both genera the cartilages of the pharyngeal arch embrace the roof and sides of the esophagus; a short muscle passes from the lower end of the ceratobranchial and ends in a band of muscle applied to the ventral face of the esophagus. The cartilages have several bands of muscle between themselves and the two sets of pharyngeal teeth. The posterior pharyngeals have a set of retractor muscles which originate above the pyloric valve in *Bathyleptus*, and above the posterior half of the stomach in *Gigantura*; these retractors pass forward between the two sheets of mesogaster and are inserted on the entire upper surface of the posterior pharyngeals. In both genera the stomach is a thick-walled blind pouch; when not distended with food

¹ If we follow the system of E. Jarvik (1954 On the visceral skeleton of *Eusthenopteron* with a discussion of the parasphenoid and the palatoquadrate of fishes. Kgl. Svensk. Vetén. Hand. (4) 5 (1): 1-104.) the anterior pharyngeal set represents the infrapharyngobranchial and the posterior set the suprapharyngobranchial elements of the same gill arch.

it is more than half the length of the body cavity and terminates shortly in advance of the dorsal fin (in both specimens of *Bathyleptus* the posterior end of the stomach is missing). The inner lining, about one-quarter to one-third the total thickness of the wall, is white and thrown into deep longitudinal folds.

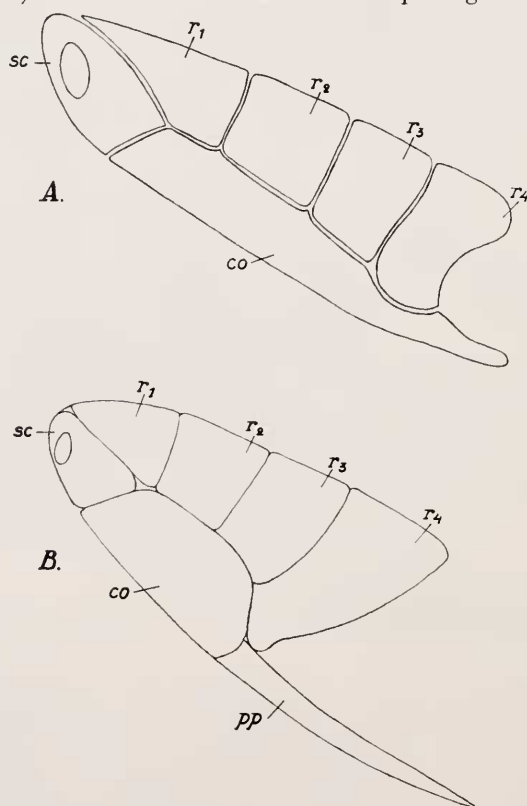


Figure 4. Left pectoral girdle in lateral aspect. A. *Bathyleptus lisae*, paratype. B. *Gigantura vorax*. Bingham Oceanographic Collection 3228. Abbreviations: co, coracoid; r_1 - r_4 , radials; pp, postcoracoid process; sc, scapula.

This is surrounded by a thick layer of intensely black material. External to the pigmented layer is the serosa. The stomach hangs in the body cavity, suspended on each side by the mesogaster, which is muscular near the esophagus. The intestine, which is colorless, leaves the pylorus near the midline, makes a few small curves along which it receives ducts from the liver and

pancreas, ascends to the dorsal part of the body cavity, passes caudad to the right of the mesogaster, turns ventrad between the unfused lobes of the ovary, and terminates in an anal papilla immediately in front of the urinogenital papilla. The course of the intestine could not be followed beyond the torn end of the stomach in *Bathyleptus*. There is one small pyloric caecum. The astonishingly small orange-colored liver consists of three lobes; in *Bathyleptus* the left-hand pair are joined while in *Gigantura* the right-hand pair are joined. In *Bathyleptus* the liver lobes are horizontal; in *Gigantura* they are vertical. In *Bathyleptus* the lobes are entire but in *Gigantura* the right pair are subdivided into lobules.

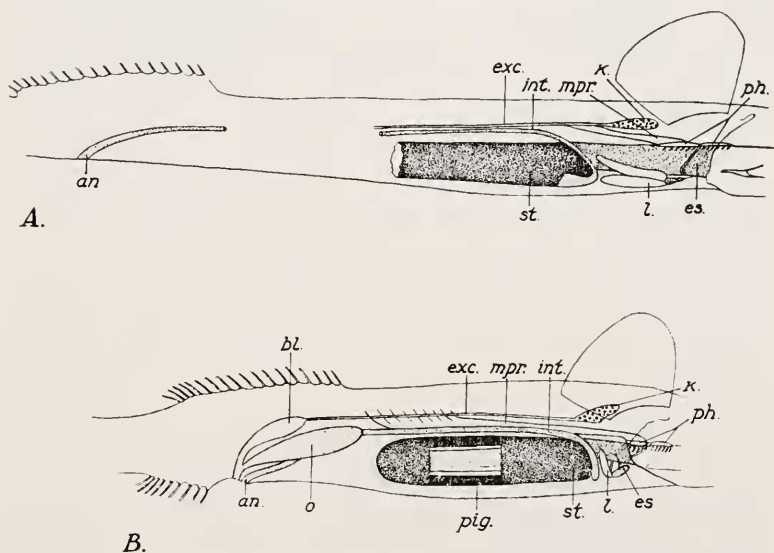


Figure 5. Visceral relations. A. *Bathyleptus lisae*, holotype. B. *Gigantura vorax*, composite drawing. Abbreviations: an, anus; bl, urinary bladder; es, esophagus; exc, excretory duct; int, intestine; k, kidney; l, lobe of liver; mpr, pharyngeal retractor muscle; o, ovary; ph, anterior and posterior sets of pharyngeal teeth; pig, deeply pigmented layer in stomach wall; st, stomach.

Circulatory System. In *Gigantura* the pericardium is embraced by the liver, the ducts of Cuvier enter the short sinus venosus beneath the middle of the ventricle, the truncus arteriosus is robust and conical, and three pairs of aortic arches arise almost simultaneously from its anterior end. In *Bathyleptus* the

pericardium is anterior to the liver, the ducts of Cuvier enter the long sinus venosus posterior to the ventricle, the truncus arteriosus is small and bulbous, and three pairs of aortic arches emerge from the short ventral aorta. In both genera the aortic arches pass forward between the pharyngeal visceral arches before turning laterally and dorsally toward the gills. In both genera the thyroid gland is anterior to the ventral aorta, and apparently has no connection with the esophagus.

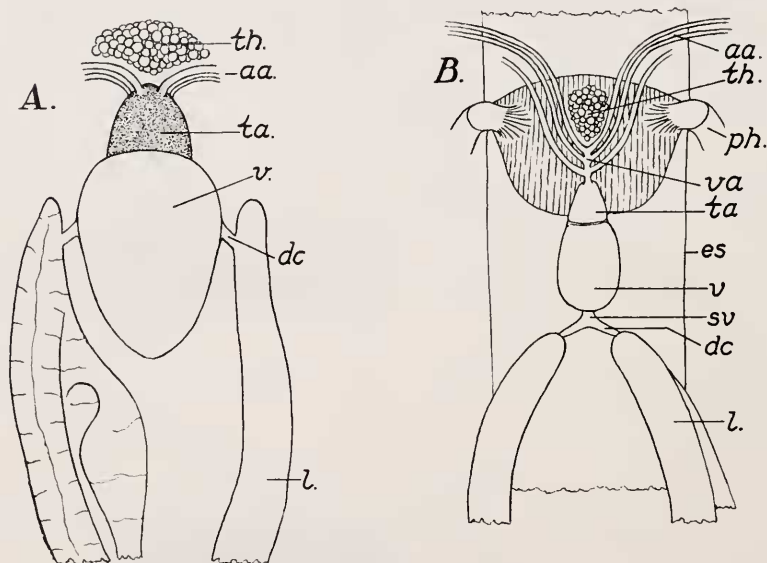


Figure 6. Heart and nearby structures in ventral aspect. A. *Gigantura vorax*, Bingham Oceanographic Collection 3228. B. *Bathyleptus lisae*, holotype. Abbreviations: aa, aortic arches; dc, duct of Cuvier; es, esophagus; l, lobe of liver; ph, pharyngeal arch; sv, sinus venosus; ta, truncus arteriosus; th, thyroid gland; v, ventricle; va, ventral aorta.

Brain, Cranial Nerves and Sense Organs. The brain of *G. vorax* has been examined. In the paratype of *B. lisae* the head and brain are crushed, but the outline of the brain is visible through the roof of the holotype skull (cf. Brauer, 1908, table 42, fig. 18 for a figure of such a view of the brain of *B. indicus*). From what can be seen, there do not appear to be any major differences between the brains of the two genera. The forebrain is very small. The enormous optic lobes are followed by the enlarged cerebellum which does not override the optic lobes.

The walls of the medulla oblongata are thickened but there are no enlarged sensory lobes. The stoutest cranial nerves are the auditory (VIII), facial (VII), trigeminal (V), and optic (II); the olfactory (I), oculomotor (III), trochlear (IV), and abducens (VI) are thread-like; the glossopharyngeal (IX) and vagus (X) are intermediate in stoutness. The pineal body is large and applied to the inner surface of the frontals near the supra-occipital; *B. lisae* has a foramen above the pineal, but in *G. vorax* the frontals are separated by a cartilaginous wedge over the pineal. The pineal stalk is remarkably long and robust; at the rear of the stalk is a pair of macroscopic habenular bodies (microscopic in most teleosts). The hypophysis has a remarkably long and slender stalk.

The labyrinth of *Gigantura chuni* was studied by Bierbaum (1914); the sacculus is smaller than the utricle. In a specimen in the American Museum of Natural History (No. 20393) the plane of the horizontal semicircular canal parallels the longitudinal axis of the head and body. The eye of *B. indicus* was described in detail by Brauer (1908); my material of *B. lisae* and *G. vorax* has not been studied in this regard. The olfactory capsule is almost microscopic and the slender olfactory nerve passes through the orbit dorsal and medial to the oblique muscles (in both genera). The lateral line system is fairly well developed on the head although difficult to trace in entirety owing to loss of skin; the infraorbital canal is particularly well developed in *Gigantura*, and is contained in flexible lightly-ossified

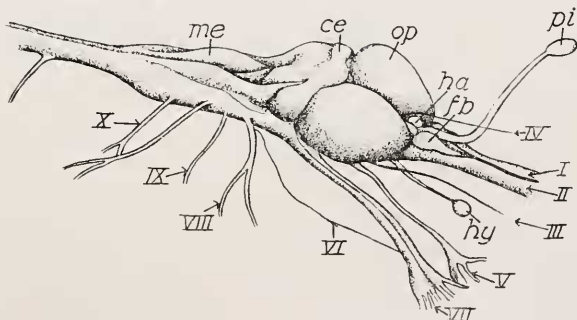


Figure 7. Brain and cranial nerves of *Gigantura vorax*, American Museum of Natural History 20393. Abbreviations: I, olfactory n.; II, optic n.; III, oculomotor n.; IV, trochlear n.; V, trigeminal n.; VI, abducens n.; VII, facial n.; VIII, auditory n.; IX, glossopharyngeal n.; X, vagus n.; ce, cerebellum; fb, forebrain; ha, habenular body; hy, hypophysis; me, medulla oblongata; op, optic lobe; pi, pineal body.

plates (? suborbitals) fringing the border of the mouth like a transparent curtain. The vagus nerve was followed along the trunk but a lateral line branch was not found; there may not be a trunk lateral line in these fishes.

BIOLOGY OF THE GIGANTURIDAE

General Considerations. The giganturids are mesopelagic predators. All of the energy in the mesopelagic fauna is derived from the photosynthetic processes of algae in the surface layers of the sea; its downward flow is mediated principally through the activities of diurnal vertical migrators which feed in the upper levels and are in turn fed upon in the lower levels. Lesser amounts of energy filter downward in the form of sinking detritus. The deeper the level at which feeding takes place, or in other words the greater the number of steps removed from the primary surface production, the smaller is the amount of food energy that is available for the biomass feeding at that particular level.¹ The size and composition of the population at any feeding level in the ocean is determined by the quantities of food energy entering and of heat leaving that population per time unit; a state of dynamic equilibrium exists and if the flow rate of energy out of the population can be reduced the result would be an increase in the biomass. The flow of energy to the physical surroundings (hence its escape from the biological system) can be attenuated by reducing the rate of metabolism. It is postulated that evolution in the mesopelagic and bathypelagic biomasses has tended toward a reduction in the rate of loss of heat energy to the physical surroundings through a reduction in the metabolic rate.

The giganturids may have achieved metabolic economies in several ways. By reducing the ossification of the skeleton, and by retaining cartilage, the density of the fish is lowered. A further reduction in density is achieved by flooding the subdermal areas with a mesenchymal jelly. Having achieved a density close to that of the surrounding water, the giganturid has no need for a swimbladder and this structure is absent.

¹ Although a mole of glucose contains about 675,000 calories, only 40 moles of pyrophosphate with an energy content of about 400,000 calories are produced when a mole of glucose is biologically oxidized to carbon dioxide and water. In other words, some 275,000 calories per mole of glucose are lost from the biomass at each link in the food chain.

Absence of the swimbladder eliminates the energy expenditure necessary (in other fishes) for the maintenance of a gas bubble at mesopelagial and bathypelagial pressures (see also Jones, 1957, p. 317).

On a wet weight basis, bathypelagic fishes which lack a swimbladder (*Gonostoma elongatum*, *Xenodermichthys copei*) have 26 to 44 per cent of the protein content of shallow water species with swimbladders (*Ctenolabrus rupestris*, *Labrus bergylta*) (calculated from Denton and Marshall, 1958: table 1). This suggests that the bathypelagic fishes have a metabolic level approximately one-third that of the coastal forms. The bathypelagic species were found to have dry weights 35 to 48 per cent that of *Ctenolabrus rupestris* (recalculated by author); therefore, the bathypelagic forms have about two and one-half times the water content of the coastal form, and, as Denton and Marshall point out, the higher water content reduces the density of the bathypelagic species. The ash of *Ctenolabrus* weighs about 1.8 to 2.4 times as much as the ash of *Xenodermichthys*, which reflects the heavier and more extensive ossification of the coastal species. Thus, Denton and Marshall's determinations are in accord with my deductions concerning the Giganturidae.

Parr (1937) suggested that the animals of the deep sea constitute a "rachitic fauna" since they are not exposed to sunlight and live with little or no vitamin D; this was offered to explain the feeble ossification of deep-sea fishes. Marshall (1955: 324-325) pointed out that abyssal benthic fishes are well ossified, while some bathypelagic forms which are poorly ossified live at levels not very far removed from the layers where vitamin D is produced. The preceding paragraphs offer an alternative explanation for the reduced ossification of some mesopelagic and bathypelagic fishes; it is likely that there are sufficient amounts of vitamin D at all levels in the ocean, maintained through the activities of vertical migrators.

It is my opinion that neoteny, indications of which are widespread in many deep-sea groups, has been one of the major avenues of evolution in the energy-poor deep-sea environment. Neoteny eliminates part or all of the mainly catabolic phase of life history, which is metabolically the most wasteful portion, and by eliminating the morphogenesis of "adult" structures neoteny may conserve additional amounts of energy for the biomass.

Sensory Cues. The enormous eyes, stout optic nerves, and large optic lobes suggest that vision is important in the giganturid life history. In contrast olfaction is of minor importance; witness the minute olfactory capsule, thread-like olfactory nerves and the minute forebrain. The other chemical sense, taste, is evidently poorly developed since there are no strong sensory enlargements in the medulla. The large cerebellum, stout auditory nerve and small sacculus are indicative of a poor auditory sense and a highly-developed sense of balance. The large trigeminal and facial nerves are partly associated with the cephalic lateral-line system which is best developed along the border of the upper jaw and apparently is of importance in feeding. The enlarged pineal body, its robust stalk, and the large habenular bodies may be associated with control of the response to variations in ambient light intensity. Rasquin (1958) discussed in detail the teleost pineal body and cited literature pertaining to the role of the pineal in governing the response to light.

Denton and Warren (1957) calculated that teleosts should be able to see daylight down to a depth of 1150 meters. This is about the lower limit at which *Gigantura chuni* was collected (660 fathoms); *Bathyleptus lisae* was taken in nets trawled at 1790 and 2140 fathoms but the actual depth of capture may have been shallower. Weale (1955) noted that since in man the threshold for light perception is 10 per cent lower for binocular vision than for monocular vision, binocular vision in deep-sea teleosts may double the visual response at illumination levels near the threshold for monocular vision. Thus giganturids, which evidently possess binocular vision, should be able to see their prey against an illuminated background throughout their vertical range. They may hunt visually at light intensity levels which are too low to enable the prey to see them well. They may follow the deep scattering layers and prey upon the luminous members of these layers, their silvery coloration allowing them to blend inconspicuously with the illuminated background.

Swimming. The small number of vertebrae (about 30) indicates that when a giganturid swims by producing lateral undulatory movements of its body it employs the carangiform rather than the anguilliform type of locomotion. The slight side-to-side movement of the head during carangiform swimming would aid in the search for food by broadening the horizontal sweep of the visual field.

The plane of the horizontal semicircular canal being parallel with the longitudinal axis of the body and the pineal body being exposed through the roof of the skull indicate that giganturids position themselves normal to the pull of gravity and normal to the path of daylight, thus probably swimming horizontally.

The long lower caudal fin lobe may stabilize forward movement in the yawing plane by lengthening the postanal part of the fish so that the dorsal and anal fins lie in the first quarter of the total length and pull rather than push the fish through the water. The asymmetry of the caudal fin would pitch the snout downward if the fin serves as a passive stabilizer and upward if it is used to propel the fish. That the long lower caudal lobe serves a passive, stabilizing role is indicated by the positions of the pectoral fin bases which are somewhat higher in front and would provide lift at the anterior end as the fish moves forward, thereby offsetting the downpitch of the asymmetrical caudal fin. The main propulsive force in swimming is apparently derived from the muscular-based dorsal, anal and pectoral fins.

Feeding. The gape of the mouth converges with the line of sight. When prey is seen, the giganturid may slowly drift in along its line of sight. When close enough so that a visual image is in proper register on the retinas of both eyes, the fish may pounce forward and seize its prey. Since the giganturid cannot see what it swallows, the last-second location of the potential food would be assumed by the infraorbital lateral line canals.

The sharp, recurved, depressible teeth indicate that once prey has been grasped there is no escape; and once it has been seized, it must be swallowed. The prey is manipulated to the rear of the mouth, perhaps through lurching and biting movements of the giganturid. Eventually the anterior set of pharyngeal teeth is able to grasp it, and their stoking actions start the food on its way down the esophagus. The posterior set of pharyngeal teeth does most of the work in packing food into the stomach, by rhythmic contractions of the powerful retractor muscles. The pharyngeal retractors are antagonized by the trunk musculature, which keeps the head and anterior trunk rigid during swallowing (although in some preserved specimens the pharyngeal retractors are contracted and the neck is distorted). The pharyngeal visceral arch is used to maintain a firm grip on the food while it is in the esophagus. In this way it would quiet the struggles of the prey and thus prevent damage to the giganturid's heart and aortic arches, which are otherwise

unprotected. The mesogaster, which is muscular anteriorly, may further aid in quieting the struggles of the prey.

Regan (1925) found a *Chauliodus* 140 mm. long in the stomach of a *Gigantura vorax* 80 mm. long. A *Gonostoma* 86-mm. long was found in the stomach of a 77-mm. *Gigantura vorax* (MCZ 35605). In both cases the tail and head of the food animal were intact while its mid-body which, to judge by its position in the stomach was swallowed first, was well-digested. These observations indicate that the giganturid requires a fairly long time to swallow a large victim. Since a 65-mm. *Gigantura vorax* (MCZ 40706) contained an intact 36-mm. *Cyclothone* sp. in its stomach, we surmise that small prey can be swallowed relatively quickly. In addition to respiratory problems which are discussed below, the giganturid is vulnerable to attack from other predators while it is engaged in swallowing luminous prey. Perhaps the giganturid packs as much as possible of the victim into its stomach as quickly as possible and then closes its mouth over the remainder which fits into the distensible, black-lined throat.

The thick deeply-pigmented layers of the distensible stomach would conceal whatever light may be emitted by the victim while it is being digested. When the food passes to the colorless intestine it is presumably no longer luminescent.

The body cavity accommodates the enormous distention of the stomach while a meal is being digested. The viscera are crowded to the anterior and posterior ends of the body cavity, out of the way of the stomach. The intestine runs dorsal to the stomach. Without such an arrangement of its organs, the giganturid would suffer intestinal strangulation and other discomforts with each hearty meal.

Respiration. The small sizes of the second, third and fourth gill slits and the absence of the gill flap from the upper end of the gill cover indicate that giganturids do not respire in normal teleostean fashion. Regan (1925) suggested that the pectoral fins fan water into the gill chamber, but this is unlikely since the gill flap would interfere while the portion which is not covered by the gill flap is anterior to the pectoral fin. Hence the giganturid probably respire by moving its suspensoria. When the suspensoria expand, some water enters the gill chamber from the pharynx via the first gill slit, when the fish is not feeding. Water can also enter the gill chamber from the outside anterior to the pectoral fin and gill flap. During inspiration the flexible flap would be pressed against the body wall. Since the pectoral

fin base projects forward in the gill chamber over two sets of gills, movements of the fin muscles could aid in mixing the water in the chamber and bathing the gills. During expiration the gill flap lifts away from the body wall and water leaves along the entire length of the gill cover. The beating of the pectoral fins wafts the water downward, backward, and away from the gill chamber. While engaged in swallowing, the giganturid would not obtain any oxygenated water via the pharynx; all would come from the outside.

SYSTEMATIC POSITION OF THE GIGANTURIDAE

Brauer (1901, 1906) compared *Gigantura* (and *Bathyleptus*) with the original description and figure of *Stylephorus chordatus*, later shown to be an allotriognath. Regan's (1925) derivation of the Giganturidae from the Synodontidae is discussed below. Berg (1940) named the order Giganturiformes, following Regan in part. Tchernavin (1947a) corrected Berg's diagnosis of the order and compared *Gigantura* with the *Lyomeri* without success because the anatomy of *Gigantura* was not well enough known. Fowler (1936, 1958) combined *Gigantura* and *Stylephorus* in one suborder; I have examined *Stylephorus chordatus* and cannot agree with Fowler. Bertin and Arambourg (1958) placed the Giganturiformes between the Synbranchiiformes (*sic*) and Saccopharyngiformes (= *Lyomeri*) without presenting any new information.

Adult giganturids possess certain features which are associated with early developmental stages in other teleost groups: the kidney is anteriorly placed; the fin-rays are not segmented; copious amounts of mesenchymal jelly underlie the skin; scales are absent; the cartilaginous endocranium persists; a vagal portion of the lateralis system seems to be absent; bones and cartilages are absent from the gill supports; there are no gill rakers; the dermal elements of the pectoral arch are missing; and the pectoral girdle has a posteoracoid process; the ventral elements of the hyoid arch, including branchiostegal rays, are missing; various dermal bones of the skull are missing such as parietals, opisthotics, and premaxillae. Thus, the Giganturidae show evidence of having become neotenic or larvalized.

Gosline (1959) thought it strange that neoteny is rare in teleosts. Actually it is not. Extreme cases of nearly complete larvalization, such as in *Schindleria*, are seldom found, but there is a broad transition zone from this one extreme to the

other in which the adult differs considerably from the immature stages (e.g., eels). The Giganturidae belong in this transition zone. The manifestation of neoteny, whether slight or considerable, implies that relationships of the group cannot be assessed unless the comparisons are confined to similarities or dissimilarities in ontogenetically equivalent structures.

If those features which appear to be neotenic were momentarily left out of consideration, the Giganturidae may be looked on as mesopelagic synodontoids. ("Synodontoid" = belonging or allied to the series of families Synodontidae-Bathysauridae-Harpadontidae.) In fact, Regan (1925) derived the giganturids from the synodontids, and there is a superficial resemblance due mainly to the backward extension of the jaws in both groups; the suspensoria have become backwardly-directed, evenly-curved arches and their caudad swing has rotated the bones of the gill cover so that the subopercular excludes the opercular from the hind margin of the gill flap, and the pharyngeal teeth now lie between the suspensoria. In the Harpadontidae (*Harpadon nehereus*, *H. microchir*), the pectoral girdle approaches the giganturid condition in that the posttemporal connects to the skull by muscle instead of a bone-to-bone contact, but the harpadontid girdle is still well developed and has all elements. Regan's assessment of the relationships of the Giganturidae might have been different had he noted the weakly-ossified lamina which lies buried in the cheek above and behind the "premaxilla"; apparently, this lamina was lost during the preparation of Regan's material.

The feature which distinguishes the iniomous fishes from less advanced teleosts is that the maxillae are excluded from the gape by the premaxillae, which alone border the upper jaw. The dentigerous bone in the upper jaw of the Giganturidae was identified by Regan (1925) as the premaxilla, but by Berg (1940) as the maxilla. Actually this bone might conceivably be any one of the following: 1) premaxilla, 2) maxilla, 3) fused premaxilla and maxilla, 4) autopalatine. The "premaxillae" of *Gigantura* and *Bathyleptus* have the following characteristics: they do not meet anteriorly, they attach anteriorly to the vomer and mesethmoid and posteriorly to the ectopterygoids, and they do not border on the posterior quarter of the upper jaw. Since the "premaxillae" do not border the upper jaw in its entirety, and since there is a separate ossification behind each "premaxilla," possible identifications (2) and (3) seem unlikely.

Consequently, the "premaxilla" appears to be the autopalatine, which would account for its anterior and posterior points of attachment to the skull, and which would also explain the apparent absence of palatines, as reported by Regan. If this interpretation is correct, the premaxillae have been lost by the Giganturidae. The small ossification behind the autopalatine is not likely to be premaxilla owing to its position; one would not expect the distal, free end of the bone to be retained while the proximal, articular end is lost. The small ossification behind the autopalatine is thus identified as the maxilla. This line of reasoning leads to the conclusion that the Giganturidae are sub-iniomes.

Non-identity of the Giganturidae with the iniomes, and identity with the sub-iniomes, is suggested also by the presence in *Bathyleptus* and in *Gigantura* of a gap between the hyomandibular and the preopercular; a muscle passes downward from the cranium through this gap to insert on the lower jaw. In none of the synodontoids has such an arrangement been noted, but there is a similar gap and muscle in *Esox lucius* and in *Argentina* (placed by Berg, 1940, in the Clupeiformes). It would be interesting to learn how many teleost groups have this muscle, and whether it may be of any phylogenetic significance.

The Giganturidae are considered here as representing an order Giganturoidea characterized as follows: upper jaw bordered by autopalatines and maxillae; premaxillae absent; maxillae not attached to skull; anterior myodome absent, posterior myodome present; orbitosphenoid, opisthotics, parietals absent; suspensorium directed backward as an evenly-curved arch; a lower jaw muscle passing through the preoperculo-hyomandibular gap; pectoral girdle free of skull and lacking posttemporal, supra-cleithrum, cleithrum and mesocoracoid; pelvic girdle absent; ventral parts of hyoid and branchial arches, including branchiostegal rays and symplectic, absent; pseudobranch, three holobranchs, one hemibranch; no gill rakers; pectoral fin base projects into gill chamber.

The relationship of the Giganturoidea to other teleosts is vague. It seems likely, however, that they belong somewhere between the esocoid members of the Isospondyli and the synodontoid members of the Iniomi.

Considering now the relationships of the Giganturoidea to higher teleost groups, Regan (1925) suggested they may be a

specialized offshoot from a line that led to the gulper eels, order Lyomeri (= Saccopharyngiformes). The magnificent studies of Tehernavin (1947a, 1947b) on *Saccopharynx* and *Eurypharynx* indicate many trenchant differences between the Lyomeri and Giganturoidea; Lyomeri have no supraoccipital, a bone which is well developed in Giganturoidea; Lyomeri have a special abductor mandibulae muscle while Giganturoidea have the usual depressor mandibulae muscle; Lyomeri have five or six holobranchs while Giganturoidea have three; Lyomeri have a single kidney, whereas Giganturoidea have paired kidneys; in Lyomeri the pectoral muscles originate on the pericardium, but in Giganturoidea the pectoral girdle is not associated with the heart. Harry (1952) pointed out further that the luminous organ of the order Cetunculi (*Cetomimus*) is comparable only with the luminous organ of Lyomeri. It is also noteworthy that in Cetunculi (*Cetomimus*) as in Giganturoidea the pectoral girdle is free of the skull (see above for pectoral girdle of *Harpadon*) and the stomach is deeply pigmented while the intestine is not (Parr, 1929). The skull of *Cetomimus* as illustrated by Parr (1929) is topologically not too different from the Giganturoidea. In conclusion, the Giganturoidea may be a specialized offshoot of a line that led from a sub-iniomous group such as the esocoids toward the synodontoid iniomes, and this line later may have given rise to the Cetunculi and perhaps eventually to the Lyomeri.

Family GIGANTURIDAE

In the following account, unless otherwise noted, statements concerning *Gigantura* and *G. vorax* are based upon specimens of *G. vorax* having the following standard lengths: 65 mm. (Museum of Comparative Zoology No. 40706), 77 mm. (Museum of Comparative Zoology No. 35605), 116 mm. (American Museum of Natural History No. 20393), 156 mm. (Bingham Oceanographic Collection No. 3228). Full data for these will be given in "Fishes of the Western North Atlantic," volume 4.

Diagnosis. Mesopelagic teleosts. Eyes large, tubular, directed forward. Gape of mouth extends far behind eye. Pectoral fin bases above gill openings. Pelvic fins absent. Dorsal fin behind middle of body. No adipose fin. Anal fin either partly below or entirely behind dorsal fin. Caudal fin forked and middle rays of lower lobe lengthened. Fin rays unsegmented, some

branched. Anus beneath dorsal fin. Sharp, recurved, depressible teeth on antopalatines, dentaries, ectopterygoids and upper pharyngeals. A layer of mesenchymal jelly beneath skin. Scales absent. Luminous organs absent. Coloration silvery.

Upper jaw bordered by autopalatines and maxillae. Autopalatines joined to vomer and mesethmoid anteriorly and to ectopterygoids posteriorly. Maxillae not attached to skull, but buried in upper lip behind autopalatines. Premaxillae absent. Anterior myodome absent. Posterior myodome present. Basisphenoid, pterospheoid (= alisphenoid) present. Cartilaginous endocranium persists beneath surface bones. Supraoccipital meets frontals. Orbitospheoid, opisthotics, and parietals absent. Suspensorium directed backward in an evenly-curved arch. Anterior upper pharyngeals between suspensoria. Retractor muscles of posterior upper pharyngeals originate on vertebrae dorsal to stomach. Rami of lower jaw loosely connected at symphysis. Throat a distensible membrane. Preopercular a splint applied to lower two-thirds of suspensorium. A gap between preopercular and hyomandibular, through which a muscle passes. Opercular excluded from posterior edge of gill flap by subopercular. Pectoral girdle not attached to skull: posttemporal, supracleithrum, cleithrum and mesocoracoid absent. Pelvic girdle absent. Ventral parts of hyoid and branchial arches, including branchiostegal rays and symplectic absent. One post-hyoidean arch complete, supporting both sets of pharyngeal teeth. Pseudobranch, three holobranchs, and hemibranch present; no slit behind hemibranch. No gill rakers. Pectoral fin base projects into gill chamber. Kidney close behind pectoral girdle. Swimbladder absent. Vertebrae 30-31.

Two genera, *Gigantura* Brauer 1901 and *Bathyleptus*, described below.

BATHYLEPTUS,¹ gen. nov.

Genotype. *Bathyleptus lisae*, sp. nov.

Diagnosis. Epitotics almost as large as supraoccipital. Pineal foramen present. Preethmoid cornua present. Supraorbital lateral line canal in a bony ridge running full length of each frontal. Pectoral girdle cartilaginous, with scapula, coracoid and four radials. Pharyngeal retractor muscles short and

¹ From the Greek *Bathos* = deep; *Leptos* = slender; in reference to the depth range and body shape.

slender, originating on fifth or sixth vertebra. Visceral arch supporting pharyngeal tooth-plates connects with strap of longitudinally striated muscle on ventral surface of esophagus. Gill openings and three holobranchs extend onto throat. Sinus venosus anterior to liver. Trunk vertebrae several times longer than wide. Trunk pencil-shaped. Caudal peduncle depth equal to or less than its width. Least caudal peduncle depth 29-51 in standard length.

Comparison with Gigantura. The diagnosis of *Gigantura* which is given below follows the form used for *Bathyleptus*. Since the two accounts are mutually exclusive it is unnecessary to present a side-by-side comparison of the genera.

Gigantura Brauer, 1901. The epiotics are considerably smaller than the supraoccipital. There is no pineal foramen. Preethmoid cornua are absent. The supraorbital lateral line canal is in a bony ridge on each frontal between the orbits but the ridges do not extend much posterior to the orbits. The pectoral girdle contains an ossified scapula, ossified coracoid, cartilaginous post-coracoid process, and four ossified radials; the fin-rays are inserted on the radials. The pharyngeal retractor muscles are long and robust, and originate on the 12th through 16th vertebrae. The visceral arch which supports the pharyngeal tooth-plates connects with a strap of transversely striated muscle on the ventral surface of the esophagus. The gill openings and gills are situated entirely above the jaws. The sinus venosus lies between the lobes of the liver. The trunk vertebrae are about as long as they are wide. The trunk is heavy and compressed. The caudal peduncle is at least 1.5 times deeper than it is wide. The least depth of the caudal peduncle is contained 11 to 16 times in the standard length.

Species. Three nominal species are placed in *Bathyleptus*. See the remarks on *Gigantura indica* Brauer and *Gigantura gracilis* Regan in the diagnosis of the following species.

BATHYLEPTUS LISAE, sp. nov.

Figure 1

Holotype. Scripps Institution of Oceanography No. H51-375; September 15, 1951; eastern Pacific north of Hawaii at 31°54'-31°36'N., 152°21'-152°03'W.; 1790 fathoms with 10-foot Isaacs-Kidd midwater trawl; R/V HORIZON, R. L. Wisner; 168 mm. standard length.

Paratype. Scripps Institution of Oceanography No. H51-377; September 23-24, 1951; eastern Pacific north of Hawaii at 31°01'-31°09'N., 127°39'-127°24'W.; 2140 fathoms with 10-foot Isaacs-Kidd midwater trawl; R/V HORIZON, R. L. Wisner; head crushed, about 127 mm. standard length.

Description. D 17-18; A 14-15; P 37-38; C 17-18; vertebrae ca. 30-31; 10 enlarged autopalatine teeth on each side; 2 ectopterygoid teeth on each side. Fin counts include all elements; italicized values are for the holotype.

Proportional measurements as per cent of the standard length (values for holotype italicized): head length to rear angle of jaws 13.7; head width across sphenotics 6.0; autopalatine length 8.7; body width at dorsal origin 3.0, 4.7; body width at middle of caudal peduncle 2.1, 3.5; body depth at dorsal origin 3.6, 6.3; least depth of caudal peduncle 2.0, 2.4; snout to dorsal origin 53.6, 54.8; snout to anal origin 72.4, 74.5; snout to pectoral beginning 11.6; length of dorsal base 16.1, 19.7; length of anal base 8.7, 8.9; length of pectoral base 6.0.

Diagnosis. The new species somewhat resembles *Gigantura chuni indica* Brauer (1901) of the Indian Ocean and *Gigantura gracilis* Regan (1925) of the tropical Atlantic, both of which are herewith transferred to *Bathyleptus* since they have extremely shallow caudal peduncles. *Bathyleptus gracilis* may be a synonym of *B. indicus*. The new species differs from the others as follows: in *lisae* the anal fin is completely behind the dorsal fin whereas in *gracilis* and *indicus* it begins beneath the rear portion of the dorsal fin; in *lisae* the anal fin base is longer than the pectoral fin base whereas it is shorter than the pectoral fin base in *gracilis* (condition unknown for *indicus*); *lisae* has 37-38 pectoral fin-rays versus 39-41 in *gracilis* and 40-43 in *indicus*.

The new species is named after my wife, Lisa.

LITERATURE CITED

BERG, L. S.

1940. Classification of fishes both recent and fossil. Trav. Inst. Zool. Acad. Sci. U. R. S. S., 5(2): 87-517.

BERTIN, L. AND C. ARAMBOURG

1958. Super-ordre des Téléostéens (Teleostei). In P.-P. Grassé (ed.), Traité de Zoologie (Paris), 13(3): 2204-2500.

BIERBAUM, G.

1914. Untersuchungen über den Bau der Gehörorgane von Tiefseefischen. Zeitschr. Wiss. Zool., 111: 281-380, 2 pls., 17 figs.

BRAUER, A.

1901. Über einige von der Valdivia-Expedition gesammelte Tiefseefische und ihre Augen. Sitzber. Ges. Beförderung ges. Naturwiss. Marburg, No. 8: 115-130.
1906. Die Tiefseefische. 1. Systematischer Teil. Jena, 432 pp. Wiss. Ergeb. deutsch. Tiefsee-Expedition "Valdivia" 1898-1899, Vol. 15. (Giganturidae, pp. 310-312, *Gigantura chuni*, pl. 1, figs. 1-3.)
1908. II. Anatomischer Teil. *Ibid.*, 266 pp. (*Gigantura indica*, pp. 213-215, pl. 42, figs. 18-21; pl. 43, figs. 1-9.)

DENTON, E. J. AND N. B. MARSHALL

1958. The buoyancy of bathypelagic fishes without a gas-filled swimbladder. Jour. mar. biol. Assoc. United Kingdom, **37**: 753-767.

DENTON, E. J. AND F. J. WARREN

1957. The photosensitive pigments in the retinae of deep-sea fish. *Ibid.*, **36**: 651-662.

FOWLER, H. W.

1936. The marine fishes of West Africa. Bull. Amer. Mus. Nat. Hist., **70**(1): 605 pp.
1958. Some new taxonomic names of fishlike vertebrates. Notulae Naturae, No. 310, 16 pp.

GOSLINE, W. A.

1959. Four new species, a new genus, and a new suborder of Hawaiian fishes. Pacific Sci., **13**: 67-77.

HARRY, R. R.

1952. Deep-sea fishes of the Bermuda Oceanographic Expeditions. Families Cetomimidae and Rondeletiidae. Zoologica, **37**: 55-72.

JONES, F. R. II.

1957. The swimbladder. Chapter IV. In M. E. Brown (ed.) The physiology of fishes. Volume II. Behavior. Academic Press, Inc., New York.

MARSHALL, N. B.

1955. Studies of alepisauroid fishes. Discovery Reports, **27**: 303-336.

PARR, A. E.

1929. A contribution to the osteology and classification of the orders Iniomi and Xenoberyces. Occ. Pap. Bingham Oceanogr. Coll., No. 2, 45 pp.
1937. Concluding report on fishes. Bull. Bingham Oceanogr. Coll., **3**(7): 1-79.

RASQUIN, PRISCILLA

1958. Studies in the control of pigment cells and light reactions in recent teleost fishes. Part 1. Morphology of the pineal region. Part 2. Reactions of the pigmentary system to hormonal stimulation. Bull. Amer. Mus. Nat. Hist., **115**(1): 1-68.

REGAN, C. T.

1925. The fishes of the genus *Gigantura*, A. Brauer; based on specimens collected in the Atlantic by the 'Dana' Expeditions, 1920-22. Ann. Mag. Nat. Hist., (9)**15**: 53-59, 1 pl., 4 figs.

TCHERNAVIN, V. V.

- 1947a. Six specimens of *Lyomeri* in the British Museum (with notes on the skeleton of *Lyomeri*). Jour. Linn. Soc. London, Zoology, **41**: 287-350.
- 1947b. Further notes on the structure of the bony fishes of the order *Lyomeri* (*Eurypharynx*). *Ibid.*, **41**: 377-393.

WEALE, R. A.

1955. Binocular vision and deep-sea fish. Nature (London), **175** (4466): 996.